

THE LACINIA IN THE MAXILLA OF THE HYMENOPTERA.*

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The maxilla of biting insects consists of six pieces. There is at the proximal end a two segmented cardo (*c*), which articulates the maxilla to the head capsule (Figs. 1 and 2†). Attached to the distal end of the cardo there is in the cockroach (Fig. 1) a rhomboidal-shaped piece, the stipes (*s*). The stipes in the locust (Fig. 2) is also rhomboidal in outline but is limited in its articulation to the mesal portion of the cardo. There is borne at the distal end of the stipes in the cockroach a two-segmented, somewhat bent tongue-shaped piece, the galea, (*g*). The galea of the locust is also two-segmented but borne at the distal and lateral margin of the stipes. At the proximal end of the galea against the lateral margin of the stipes, there is a small sclerite, the palpifer (*p*), which bears the five segmented maxillary palpus. The proximal segment of the galea and the palpifer in the locust constitute the lateral margin of the stipes. There is borne at the distal end of the stipes on the mesal side another appendage, which bears three prominent teeth at its distal end. This is the lacinia (*la*). The arrangement of the parts in the maxillæ of biting insects is for all practical purposes identical with the above description and the figures of the maxillæ of the cockroach and the locust, showing two distal pieces, a lacinia on the mesal side and a galea on the lateral side, with a segmented maxillary palpus attached on or near the lateral margin at the proximal end of the galea, and is characteristic.

If the maxilla of *Macroxyela infuscata* (Fig. 3), one of the most generalized members of the order Hymenoptera, a tenthredinid, known to me, is compared with that of the cockroach

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†The cardo of *Melanoplus differentialis* as here figured shows a narrow proximal piece with two projections at its proximal end; the shorter piece articulates against the ectal surface of the head capsule and the larger piece passes beneath the margin of the head capsule and serves for the attachment of muscles. These pieces are characteristic of this and some other species. It has been overlooked because it usually remains attached to the head capsule when the maxilla is removed.

or locust, a somewhat similar condition is found. The cardo, however, consists of a single piece which bears at its distal end an irregular-shaped stipes. The stipes bears at its distal end on the mesal side a quadrangular-shaped sclerite, which from its position must be the lacinia. There is borne on the lateral part of the distal portion of the stipes a two-lobed piece, the galea, which consists of a larger outer and a smaller inner lobe. The suture dividing the galea into two pieces is obsolete. Although not demonstrable, it is quite likely that the small mesal lobe of the galea is derived from the proximal sclerite of the galea and the large lateral lobe from the distal sclerite of the galea. The palpifer and maxillary palpus occupy corresponding positions to these sclerites in the cockroach. The maxilla of *Macroxyela* is short and broad and retains many of the general features and appearances of the maxillæ of the cockroach and locust.

The maxilla of *Dolerus unicolor* (Fig. 4), another tenthredinid, differs from that of *Macroxyela* in that it shows some of the tendencies so characteristic of the maxillæ of the higher Hymenoptera, an elongation and narrowing of the parts. This is especially marked in the cardo of *Dolerus*. The maxilla of *Dolerus* also has three lobes at the distal end. The rounded setaceous lateral portion is the homologue of the large lateral lobe of the galea of *Macroxyela*, while the mesal and proximal rounded lobe is the homologue of the small mesal lobe of the galea of *Macroxyela*. The lacinia is a long, pointed lobe projecting beyond the mesal lobe of the galea but attached to the stipes beneath this lobe of the galea. *Dolerus* is a comparatively generalized tenthredinid yet it shows an early stage in the migration of the lacinia from the distal end of the maxilla. A somewhat similar condition is shown in the maxilla of an ichneumonid, *Ophion bilineatum* (Fig. 5). The two lobes of the galea are large, the mesal lobe is a broad flat plate and almost completely covers the lacinia, which is a broad lobe attached to the side of the stipes. The lateral lobe of the galea is elongated and terminal as in the higher Hymenoptera.

In the white faced hornet, *Vespa maculata* (Fig. 6), the maxilla shows a decided elongation of all the parts, the cardo, stipes, and lateral lobe of the galea. The sclerites are not all arranged in the same plane as with the maxillæ previously described. This is due to the fact that the maxillæ are closely appressed to the sides of the convex labium or lower lip, which

has changed somewhat the orientation of the parts. The galea is almost as long as the elongated stipes and is composed for the most part of a large lobe which is the homologue of the lateral lobe of the galea of the maxillæ previously described. The homologue of the mesal lobe is much smaller and has changed its position somewhat. It is a small lobe placed on the surface of the larger, lateral lobe, nearer its lateral than its mesal margin. The mesal margin of the small, mesal lobe is marked by a row of long setæ. All the sutures between the parts of the galea and the stipes are obsolete. There are several dark and light areas with oblique ridges where they probably fuse, but specimens prepared with caustic potash show no indication of a suture in this region. The lacinia is a small but well marked lobe attached to the mesal margin of the proximal end of the stipes. Its position is clearly indicated in figure 6. The distal end of the lacinia is usually folded under the proximal end of the galea and more or less concealed. It shows distinctly on unmounted specimens studied in alcohol.

A thread-waisted wasp, *Sphex pennsylvanicus* (Fig. 7), shows a somewhat different condition. In the maxilla of this insect the small, mesal lobe of the galea is wanting and the lateral lobe developed into a greatly elongated, blunt piece, which projects for some distance beyond the stipes and is almost as long as the maxillary palpus. There is a groove along the lateral margin of the galea that may mark the line of separation of the small, mesal lobe of the galea. Unfortunately it was not discovered until it was too late to remedy the defect, that the figure of this maxilla was turned in the opposite direction from the others. The lacinia is located at the proximal end of the galea in this maxilla. It is a broadly rounded lobe. Its location and the development of the proximal end of the galea as an overhanging projection would suggest that the lacinia had been modified into a supporting piece.

The greatest modification of the maxillæ is found with the bees where they have been greatly elongated into plates for close appression against the labium for the formation of a tube. The maxilla of a bumble bee, *Bombus terricola* (Fig. 8), shows this condition well. The galea is a sword-shaped blade as long as the remainder of the maxilla. It is attached to the distal end of the stipes. The two are fused without any indication of a suture. There is an oblique ridge marking the edge of a deep

furrow with lighter intervening parts. It is likely that this oblique, clear area distad of the ridge marks the distal limit of the stipes. This would make the union between the stipes and galea an oblique one with the maxillary palpus attached to the distal prolongation of the stipes. A similar condition will be noted in the other maxillæ figured. The furrow extending across the maxilla is the limit of the distal part of the maxilla that is folded under the labium. If this ridge be considered as the suture between the stipes and the galea, it would place the maxillary palpus on the galea, which is an impossible interpretation in the light of the other maxillæ studied. In the more specialized Hymenoptera, wasps and bees, there is a cuticular membrane connecting the maxilla and the labium, which serves to close the mouth cavity on the ventral side. The distal edge of this membrane is attached to the stipes near the proximal end of the lacinia. This membrane is particularly well marked in mounts of the entire maxilla and labium of *Bombus*. In such mounts, the lacinia can be identified as a round lobe with long setæ on its distal and lateral margins. It is placed adjacent to the distal margin of the membrane extending from the maxilla to the labium and is attached to the mesal margin of the stipes near its distal end or to the uncolored area of the stipes. This lobe is so distinct, once it has been seen, it is hard to understand how it has remained undescribed for so long. The lacinia, while showing distinctly in specimens mounted in balsam, can be studied to better advantage on maxillæ that have been cleared in caustic potash and examined in a watch glass in alcohol.

Insect morphologists have been fairly uniform in their statements regarding the lacinia in the honey bee, *Apis mellifica* (Fig. 9). All the more important text-books on entomology figure a maxilla of *Bombus* or *Apis*, but without indication of the lacinia. The following quotations are typical for the maxilla of *Apis*. Comstock and Kellogg* describe these parts as follows:

"*Stipes*. The stipes is an irregular, elongate sclerite, strongly chitinized. Its proximal end is bluntly rounded and swollen. The stipes articulates with the proximal segment of the galea (see below) by a diagonal face.

*Comstock, John Henry and Kellogg, Vernon L. The elements of insect anatomy. Ithaca. 1901. Pp. 78-79.

"*Galea*. The *galea* (we incline to believe this part homologous with the *galea* of the locust's maxilla, rather than with the *lacinia*, because of its two-segmented condition) extends distad from the *stipes* as a tapering blade-shaped piece. It is composed of two segments. The proximal one is small and triangular, articulating by the entire length of one of its margins with the *stipes*. The distal segment or sclerite constitutes the real blade-like portion of the maxilla, and nearly equals in length the *ligula* and *labial palpi* (see below). Its surface is unequally divided into two portions by a submedian, dark-brown, longitudinal line. (This line may indicate a coalescence of *galea* and *lacinia* into this one blade-like compound sclerite). This line bears several hairs, and there are scattering hairs elsewhere on the sclerite, especially toward the distal end."

Snodgrass† writes as follows of the maxilla of the honey-bee:

"Let us now return to a study of figure 15D. The series of lateral pieces as already explained are the maxillæ. A comparison with figure 3B representing a generalized maxilla will show that these organs in the bee have suffered a greater modification than has the labium, but the parts can yet be quite easily made out. The main basal plate (*st*) is the combined *stipes*, *subgalea*, and *palpifer*, the basal stalk is the *cardo* (*cd*), and the little peg-like process (*mx plp*) at the outer end of the *stipes* is the greatly reduced *maxillary palpus*. Hence, we have left only the terminal blade-like lobe (*mx*) to account for, and it is evident it must be either the *galea* or the *lacinia* (See fig. 3B, *ga* and *lc*) or these two lobes combined. Here again a comparative knowledge of the mouth parts of Hymenoptera comes to our aid and shows clearly that the part in question is the outer lobe or *galea*, for the inner one becomes smaller and smaller in the higher members of the order and finally disappears."

There is expressed in these two quotations very different views, the former that the *galea* and *lacinia* are probably coalesced and the latter that the *lacinia* is wanting. This is the status of the *lacinia* in the higher Hymenoptera, writers consider it either as fused with the *galea* or as obsolete.

A comparison of the drawing of the maxilla of the honey bee with that of *Bombus* shows it to be similar in form but shorter and consists of a long, slender, proximal piece, the *cardo*,

†Snodgrass, R. E.—The anatomy of the honey bee. U. S. Dept. Agr., Bur. Entom., Tech. Ser. No. 18, 1910. Pp. 45-46.

and a distal piece divided into two regions by the difference in coloration. The distal two-thirds is a blade-shaped piece with a median ridge bearing setæ. This blade-shaped piece is the galea and the median ridge is the supposed line of coalescence of the galea and lacinia of Comstock and Kellogg. There is borne on the lateral margin at the proximal end of the galea a two-segmented appendage, the palpifer and a one-segmented maxillary palpus. The palpifer is inserted in a furrow in the side of the maxilla and can be pushed back against the bottom of this furrow so as not to project beyond the lateral margin of the maxilla. There is a distinct convexity at the distal end of this furrow and an oblique line extends across the maxilla from this point, which probably marks the division between the galea and the proximal piece of this portion of the maxilla, the stipes. The suture between the galea and stipes is obsolete. The lacinia is a thin, cuticular lobe attached near the mesal margin of the stipes at its distal end. It is not attached at the margin of the stipes but a short distance within. The lacinia at its distal margin is developed into a lobe which rests upon the base of the galea. It is so delicate that where it rests upon the galea, its distal end appears like a faint, curved, transverse suture. The distal end of the lacinia resting upon the galea is evidently what Comstock and Kellogg have mistaken for a suture separating the galea into a triangular proximal piece and a distal blade-like piece. The lacinia is larger and more distinct in the honey bee than in *Bombus*. It shows very distinctly on specimens cleared in caustic potash and studied in alcohol.

The lacinia was found to be present in the maxillæ of practically all the Hymenoptera examined. It is very large and distinct in *Priocnemis*, fully one-third the size of the galea which is greatly expanded and consists of two distal lobes. In the large carpenter ant, *Campanotus*, the lacinia is a distinct lobe at the proximal end of the galea. Wheeler* considers it as present but his figures of the maxillæ copied from Janet do not show it. A species of *Andrena* also shows it as a lobe similar in form and location to that of *Bombus* and *Apis* but smaller. The only hymenopterous insect examined where the lacinia was found to be completely wanting was the short tongued bee,

*Wheeler, W. M.—Ants, their structure, development, and behavior. New York. 1910. P. 19.

Augochlora. In this bee the galea has been reduced to a mere oblique knob at the distal end of the maxilla and the stipes transformed into a blade-shaped organ with a distinct palpifer and a five segmented maxillary palpus on the lateral margin near the distal end of the maxilla.

LIST OF ABBREVIATIONS.

- c. Cardo.
- c1. Proximal segment of cardo.
- c2. Distal segment of cardo.
- g. Galea.
- g1. Distal segment of galea.
- g2. Proximal segment of galea.
- la. Lacinia.
- mp. Maxillary palpus.
- p. Palpifer.
- s. Stipes.

PLATE XVIII.

(Drawings by Alvah Peterson.)

1. *Periplaneta orientalis*.
2. *Melanoplus differentialis*.
3. *Macroxyela infuscata*.
4. *Dolerus unicolor*.
5. *Ophion bilineatum*.
6. *Vespa maculata*.
7. *Sphex pennsylvanicus*.
8. *Bombus terricola*.
9. *Apis mellifica*.